

The transition from mainland to island, illustrated by the flora and landbird fauna of headlands, peninsulas and islands near Albany, Western Australia*

by Ian Abbott

Zoology Department, University of Western Australia, Nedlands, W.A. 6009
(Present address: Institute of Forest Research and Protection, Hayman Road, Como, W.A. 6152)

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Abstract

Lists of species of plants and landbirds present on 11 islands and 17 coastal mainland sites near Albany have been used in regression analyses to study how the floras and landbird faunas of islands come to differ from those of coastal mainland areas. For a particular area or elevation, plant species richness decreases as follows: mainland areas sheltered from prevailing swell, mainland areas fully exposed to prevailing swell, sheltered islands, exposed islands. These differences become more pronounced the larger the area or the higher the land. It is suggested that most extinctions on these islands result from the action of storm waves and continual deposition of seaspray, the low frequency of fires and the presence of colonially-nesting seabirds. The number of landbird species decreases in the following sequence for any particular sized area: sheltered mainland, sheltered island, exposed mainland, exposed island. This reflects mainly changes in the extent of forest, determined largely by exposure to seaspray. These gross differences between coastal mainland areas and islands are paralleled on representative 4 ha plots. Attention is drawn to interesting, particularly puzzling, distribution patterns of selected native plant species and landbird species. The distribution of weed species on the islands and coastal mainland sites is interpreted in terms of a dynamic equilibrium dependent on introduction by European man and Silver Gulls and establishment on nutrient-rich soils produced by colonially-nesting seabirds.

Introduction

Although biogeographic studies of floras and landbird faunas on islands have been popular since last century (e.g. Darwin 1845, Hooker 1847-1860, Moseley 1892, Wallace 1911), few such studies have been accompanied by ecological comparisons with mainland sites. Mathematical analyses over the last two decades have shown that the number of plant or landbird species present on islands can usually be closely predicted from island area (review in Abbott 1974a). Just why island floras and faunas should have fewer species than floras and faunas on equal-sized areas on the adjacent mainland has been given little attention despite the widely accepted model proposed by MacArthur and Wilson (1967). Islands, of course, have distinct boundaries whereas equal-sized areas on the mainland invariably are difficult to delineate. A coast along which there are numerous peninsulas, headlands, capes as well as islands partly overcomes this difficulty of defining boundaries. Although I have studied the floras and landbird faunas of the 121 islands near Perth (Abbott 1977, 1978a), the adjacent mainland is of uniform outline and so is unsuitable for a comparative biogeographic study of island and mainland floras and avifaunas.

The coast near Albany (Fig. 1) has a configuration admirably suited for such studies, and in addition the flora is exceptionally rich and varied, making the search for and collection of plant species very rewarding. This paper has three aims. The first is to examine how species richness for the plants and landbirds changes with diminishing area, isolation, elevation and exposure to wave action and seaspray. Because peninsulas are intermediate between islands and headlands, their study should throw light on the processes that change the flora and avifauna of a landmass as it becomes an island. Second, the composition of the plant and bird communities present on islands will be described and analysed with reference to the coastal mainland sites. Finally, the spread of weed species onto islands and coastal mainland sites by gulls and European man will be examined.

Geographical setting

The coast near Albany (Fig. 1) is a drowned one, and in the 150 km length of coast considered for this paper there is one large peninsula, two promontories and numerous smaller headlands. The bathymetry of the seas shown in Figure 1 is only known adequately in and near King George Sound; on the basis of R.A.N. Hydrographic chart No. 118 I have reconstructed the sequence of changes in coastal configuration resulting from the postglacial rise of sealevel. This, in conjunction with information provided by Hails (1965)

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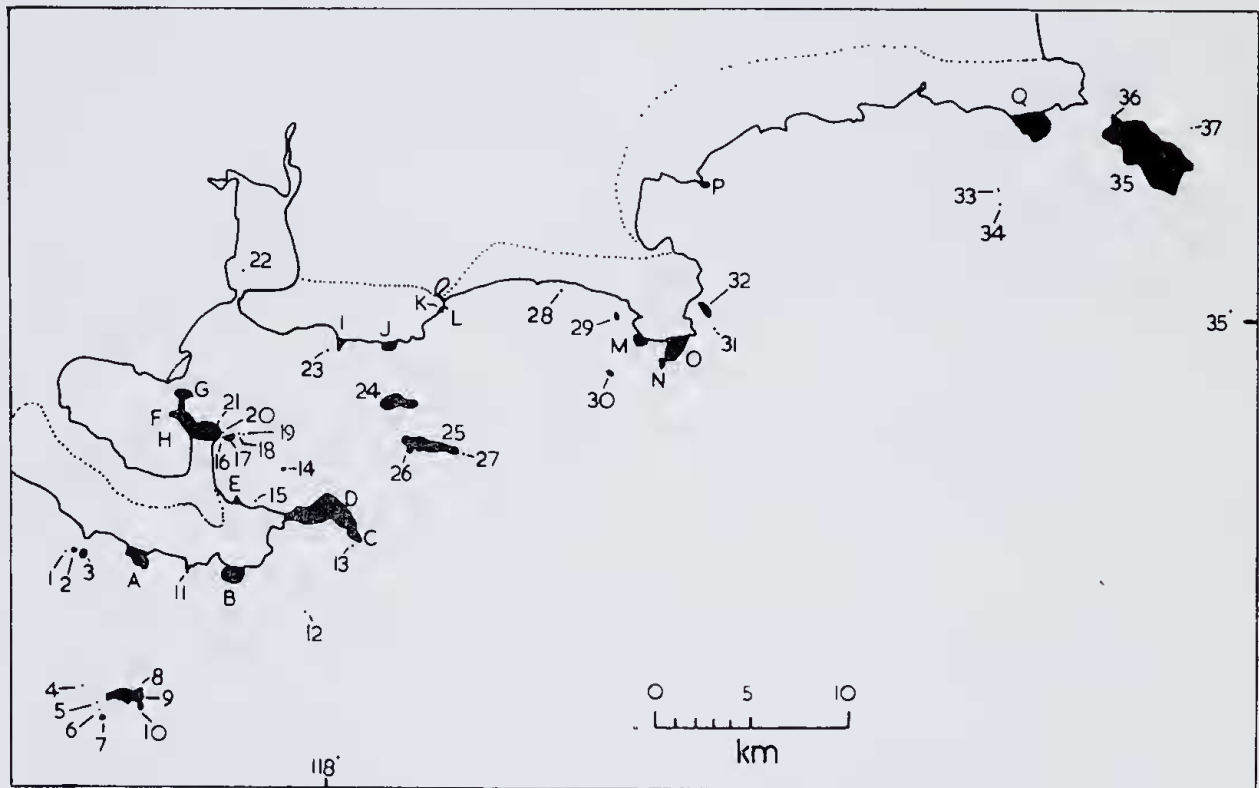


Figure 1.—Map of Albany region of south-western Australia showing coastal sites (A–Q) and all islands (1–37). Vegetated islands numbered 2, 3, 6, 29, 30 were not visited. The dotted line represents the approximate southern boundary of farming or settlement.

and Thom and Chappell (1975), indicates approximately when the largest islands became isolated: Eclipse Island (13 000 yr BP), Breaksea Island (9 000 yr BP) and Michaelmas Island (7 000 yr BP). Bald Island became isolated 10 000 yr BP (Storr 1965).

The region has an indented coastline with precipitous cliffs, mainly of adamellite and gneiss (Stephenson 1973, 1974), alternating with smooth sandy beaches (Jutson and Simpson 1917). All islands, however, lack sandy beaches although cobble and boulder beaches of limited extent are found on the lee (northern) sides of Bald, Eclipse, Michaelmas and Breaksea Islands. The Vancouver Peninsula (GH in Fig. 1) has been formed by deposition of windblown sand between two islands and the mainland (Jutson and Simpson 1917), probably after 6 000 yr BP. The ridge between Bald Head (C in Fig. 1) and Torbay Inlet, as well as the Mt Gardner complex, have also been tied to the mainland by the silting up of swamp and deposition of sand. The gneiss and adamellite are overlain by aeolianite in certain areas (see Table 1).

The soils are shallow sands (Northcote *et al.* 1967); those over adamellite, gneiss or granite have a pH of 3–5, whereas those over aeolianite are of pH 6–8 (from samples collected on Eclipse and Breaksea Islands). Further details of these soils are provided for Chatham Island by Abbott and Watson (1978).

The climate of the region is typically Mediterranean. Data from Breaksea and Eclipse Islands (Anon 1975; unpublished records of Bureau of Meteorology) show that the islands have lower maximum temperatures and higher minimum temperatures and receive over 100 mm less rain annually than the nearest recording stations near Albany. For the area shown in Figure 1 there is a rainfall gradient decreasing from west to east of about 1 000 mm to 750 mm annually. This is reflected

in a vegetational change evident on the coast near North Point (P in Fig. 1). East of this the vegetation is dominated by low heath whereas west of North Point woodland and forest predominate.

Man's impact on the environment is well documented. The Albany area was occupied by Aboriginal man when discovered by Europeans in 1791 (Vancouver 1801). These people extensively and regularly used fire in their hunting (Hallam 1976). As they did not possess watercraft (Flinders 1814) and could not swim (Nind 1831), the islands were unvisited and so escaped frequent firing of the vegetation. European man now farms much of the hinterland (Fig. 1), but because of the poor soils near the coast none of my mainland sites has ever been farmed or cleared, and few have been grossly tampered with. Fishing tracks or roads have been cut through most of these sites. European man, has, however, had more impact on the habitats of the larger islands; this began in the 1820s when sealers arrived (Cumpston 1970) and doubtless involved fires (e.g. Lockyer 1827) and certainly affected some plant and animal populations (see later). Breaksea Island had a manned lighthouse between 1858 and 1926, and Eclipse Island had one between 1926 and 1976. Limited clearing of vegetation occurred, and the presence of one or two horses in the earliest days had a largely unknown effect on vegetation (Bald Island was used for agistment late last century and early this century). Some of the smaller islands have been more adversely affected: Mistaken Island was set ablaze in 1803 by the Baudin expedition (Cornelle 1974) and goats were grazed there in the 1830s (Clark 1841). Site F was formerly an islet on which a powder magazine was placed in about 1844 to prevent tampering by aborigines, but in the 1870s a causeway was constructed to it (H. Sunter-Smith 1976, pers. comm.).

Table 1

Area, maximum elevation, and total number of plant and landbird species found on mainland sites and islands studied

| Code in Figure 1 | Name (if any) | Visits | Area (ha) | Maximum elevation (m) | No. vascular plant species | No. landbird species** |
|------------------|------------------------|---|-----------|-----------------------|----------------------------|------------------------|
| Mainland Sites | | | | | | |
| A*† | Cave Pt | 22-23 Sept. 76 | 61 | 80 | 104 | 5 |
| B*† | Peak Hd | 30 Sept. 75 19 Dec. 76 | 46 | 150 | 125 | 4 |
| C* | Bald Hd | 27 Nov. 75 28 Oct. 76 | 30 | 122 | 85 | 5 |
| D*† | Flinders Pen. | 27 Nov. 75 24 Sept. 76 28 Oct. 76 | 309 | 234 | 166 | 19 |
| E | Waterbay Pt | 21 Sept. 76 9 Dec. 78 | 4 | 40 | 129 | 3 |
| F | Geak Pt | 16 Sept. 76 | 0.3 | 6 | 54 | 0 |
| G | Pt Possession | 24 Nov. 75 18-19 Sept. 76 | 17 | 46 | 164 | 10 |
| H | Vancouver Pen. | 15-25 Sept. 76 | 168 | 81 | 292 | 21 |
| I† | Ledge Pt | 25 Sept. 76 | 13 | 52 | 129 | 4 |
| J† | Herald Pt | 26 Oct. 76 | 25 | 69 | 160 | 7 |
| K† | Islet Pt | 21 Dec. 76 | 3 | 30 | 88 | 1 |
| L† | | 26 Nov. 75 21 Dec. 76 7 Dec. 78 | 1.3 | 23 | 56 | 2 |
| M*† | False I. | 27 Oct. 76 | 18 | 84 | 45 | 4 |
| N*† | C. Vancouver | 27 Oct. 76 | 8 | 51 | 38 | 1 |
| O*† | | 27 Oct. 76 17 Sept. 78 | 69 | 137 | 140 | 7 |
| P* | North Pt | 24 Sept. 76 | 10 | 27 | 40 | 4 |
| Q*† | Mermaid Pt | 26 Oct. 76 | 158 | 210 | 150 | 14 |
| Islands | | | | | | |
| 1* | | — | 0.004 | 6 | 0 | ... |
| 4* | Northwest Rk | — | 0.002 | 2 | 0 | ... |
| 5* | | — | 9 | 12 | 0 | ... |
| 6* | | — | 9 | 18 | 0 | ... |
| 8* | NE pen., Eclipse I. | 11-12 April 75 | 1.2 | 12 | 16 | 0 |
| 9* | Eclipse I. | 4-15 April 75 | 104 | 109 | 51 | 4 |
| 10* | Cliff Hd | — | 12 | 26 | 0 | ... |
| 11* | | — | 0.7 | 15 | 0 | ... |
| 12* | Vancouver Rk | — | 3 | 5 | 0 | ... |
| 13* | Northumberland Rk | — | 0.5 | 4 | 0 | ... |
| 14 | Seal I. | 28 Nov. 75 | 1.8 | 32 | 22 | 0 |
| 15 | Flat Rk | 28 Nov. 75 | 0.3 | 3 | 1 | 0 |
| 16 | I. next to Mistaken I. | 23 Sept. 76 | 0.08 | 4 | 31 | 0 |
| 17 | Mistaken I. | 15 Sept. 75 23 Sept. 76 | 9.9 | 44 | 61 | 2 |
| 18 | W. Sister Rk | — | 0.001 | 2 | 0 | ... |
| 19 | E. Sister Rk | — | 0.001 | 1 | 0 | ... |
| 20 | | — | 0.04 | 2 | 0 | ... |
| 21 | | — | 0.2 | 3 | 0 | ... |
| 22 | Green I. | 28 Nov. 75 | 1.7 | 12 | 30 | 0 |
| 23 | Gull Rk | 28 Nov. 75 | 2.5 | 10 | 26 | 0 |
| 24† | Michaelmas I. | 4-14 Sept. 75 | 90 | 152 | 78 | 11 |
| 25*† | Breaksea I. | 23 Aug.-1 Sept. 75 | 102 | 102 | 61 | 4 |
| 26*† | S. pen., Breaksea I. | 27-28 Aug. 75 | 2.7 | 42 | 29 | 0 |
| 27* | | — | 1.2 | 20 | 0 | ... |
| 28* | Black Rk | — | 1.5 | 12 | 0 | ... |
| 31* | | — | 0.003 | 2 | 0 | ... |
| 22* | Coffin I. | 27 May 76 | 28 | 45 | 30 | 4 |
| 33* | N. Twin It | — | 1 | 26 | 0 | ... |
| 34* | S. Twin It | — | 1 | 26 | 0 | ... |
| 35*† | Bald I. | 14-25 May 76 | 717 | 311 | 104 | 15 |
| 36*† | N. pen., Bald I. | 15-18 May 76 | 6 | 40 | 13 | 0 |
| 37* | Bird Rk | — | 0.001 | 4 | 0 | ... |

* Indicates mainland sites and islands fully exposed to the swell from the SW; the remainder are sheltered.

† Indicates mainland sites and islands with aeolianite.

** Omitting raptors and presumed vagrants.

Those islands marked—under Visits were flown over in April 1977 and some were observed from other islands or the mainland through binoculars.

Previous biological investigations of the Albany coastline are many, as King George Sound until 1900 was the major port of Western Australia. Diels (1906) and Souster (1948) provide reviews of botanical collecting in the region but for the present paper most of these collections are of limited use because the exact locality was not recorded. An important exception is L. Preiss who collected 43 plant species on several of my mainland sites in October and December 1840 (Lehmann 1844–1847). I have re-collected 27 of these and a further two cannot satisfactorily be linked with modern botanical nomenclature, leaving only eleven not accounted for. On the other hand, studies of the island floras and faunas are very limited. The early naval expeditions of Vancouver (1801), Flinders (1814), Baudin (Cornelle 1974) and King (1827) visited Seal Island and Green Island. Others provide scattered references to plants and animals (Lockyer 1827, Campbell 1890, 1900, Clark 1841). Reports published this century are those of Bassett Hull (1922), Warham (1955), Storr (1965), Fullager and van Tets (1976), Serventy and Whittell (1976) and Smith (1977a). Reference to relevant aspects of these papers will be made later.

Methods

Eleven islands and 17 coastal mainland sites (Fig. 1) were visited between 1975 and 1978 as part of a study of the ecology of the passerine bird *Zosterops lateralis* (Abbott in prep.). Visits to the 4 largest islands were each of about 12 days (Table 1), while the remaining islands were visited for between 30 minutes and 5 hours, depending on their area. Mainland sites were visited, depending on their extent, for 2–9 hours at one time. Some sites were visited more than once (Table 1). Although all islands in the region are numbered in Fig. 1, I was unable to land on five (numbers 2, 3, 7, 29, 30)—all vegetated but exposed fully to the swell.

During my visits collections of plant species were made and I kept a list of species of plants and birds present. On the 4 largest islands and on one of the mainland sites, fifty 1 m² quadrats were randomly distributed in a 4 ha plot. Landbirds were netted for study in this plot.

Results

The data base for the majority of this paper is the list of plant species and bird species found at each site (Appendices 1, 2). The total number of plant and land-bird species found at each site, along with various physical attributes of the sites, is summarized in Table 1. The total area of all islands (1 106 ha) and all mainland sites (941 ha) is remarkably similar. Despite this, the islands have fewer species of plants and land-birds than mainland sites of comparable area. The first point to establish is whether each plant family has been equally impoverished in species on the islands. Appendix 1 shows that only 15 of the 77 families found were not represented on any island: Ophioglossaceae, Dennstaedtiaceae, Lindsaeaceae, Xanthorrhoeaceae, Phylodraceae, Haemodoraceae, Olacaceae, Loranthaceae, Lauraceae, Tremandraceae, Polygalaceae, Onagraceae, Loganiaceae, Lentibulariaceae and Orobanchaceae. Two families (Aspleniaceae, Tropaeolaceae (introduced)) were found only on islands. Thus, the large-scale impoverishment of plant species on the islands represents a general impoverishment within families, and not the absence of a majority of plant families.

Seven families widespread on the mainland sites were present on only one island (Restionaceae, Casuarinaceae, Santalaceae, Phytolaccaceae, Stackhousiaceae,

Sterculiaceae, Goodeniaceae). The extent of impoverishment of plant species on the islands can be quantified in terms of those families containing 10 species or more (Table 2). Values of impoverishment range from 0 (all species represented on at least one island) to 92% (i.e. nearly all species absent from islands), with a median value of 61–66%. Impoverishment has not been random between families because some families are better represented on islands than others.

Table 2

Impoverishment of insular floras in terms of families containing 10 or more species. Alien species are excluded

| Family (No. species) | No. species found on at least one | | % impoverishment |
|--------------------------|-----------------------------------|--------|------------------|
| | mainland site | island | |
| Poaceae (11) | 10 | 7 | 30 |
| Cyperaceae (18) | 18 | 7 | 61 |
| Restionaceae (12) | 12 | 1 | 92 |
| Liliaceae (12) | 11 | 5 | 55 |
| Orchidaceae (20) | 20 | 4 | 80 |
| Proteaceae (41) | 41 | 4 | 90 |
| Chenopodiaceae (10) | 9 | 9 | 0 |
| Mimosaceae (14) | 14 | 5 | 66 |
| Fabaceae (29) | 29 | 5 | 83 |
| Dilleniaceae (10) | 10 | 1 | 90 |
| Myrtaceae (30) | 30 | 13 | 57 |
| Apiaceae (11) | 10 | 6 | 40 |
| Epacridaceae (17) | 17 | 3 | 82 |
| Asteraceae (33) | 31 | 18 | 42 |

Comparison of plant species richness

The variation in plant species richness on the mainland and islands has been analysed in terms of area, elevation and degree of exposure to the prevailing south-west ocean swell. Coefficients of correlation were calculated between area and elevation for six types of site (sheltered or exposed mainland sites, sheltered or exposed unvegetated islands, and sheltered or exposed vegetated islands) in Table 3, and between plant species richness and area and elevation for sheltered and exposed mainland sites and sheltered and exposed vegetated islands in Tables 4 and 5. These analyses were necessary to show which mathematical model best fitted the data. From Table 3, a double logarithmic model yielded the highest correlation coefficients. On the other hand, Tables 4 and 5 show respectively that a semilogarithmic and an arithmetic model are most appropriate. The appropriate mathematical model has been used to compare islands and mainland (Figs 2–4) by analysis of covariance. Details of the statistical tests made have been collected together in Table 9.

Area v. elevation (Fig. 2).—There were no significant differences in slope or intercept for the following comparisons: sheltered mainland v. exposed mainland, sheltered mainland v. sheltered vegetated islands, exposed mainland v. exposed vegetated islands, and exposed unvegetated islands v. exposed vegetated islands. Hence categories were then combined as in Figure 3. It was found that the logE/logA regression line for islands devoid of vegetation had a significantly lower slope than that for the vegetated islands but that the intercepts did not differ significantly. This graph shows that islands with an area of about 1 ha or more and elevation 7 m or higher can support at least one plant

Table 3

Area (A): elevation (E) relationships for mainland sites, vegetated islands and unvegetated islands. The correlation coefficients and their significance are shown for the four mathematical models examined

| Places | Sample size | Models | | | |
|-------------------------------|-------------|---------------|---------------------|------------------|------------------|
| | | <i>E v. A</i> | <i>ln E v. ln A</i> | <i>E v. ln A</i> | <i>ln E v. A</i> |
| Mainland sheltered | 8 | 0.73* | 0.92** | 0.98*** | 0.51 ns |
| exposed | 9 | 0.85** | 0.87** | 0.92*** | 0.70* |
| all sites | 17 | 0.80*** | 0.92*** | 0.82*** | 0.64** |
| Unvegetated islands sheltered | 4 | | | | |
| exposed | 14 | 0.43 ns | 0.76** | 0.66** | 0.47 ns |
| all | 18 | 0.51* | 0.80*** | 0.71** | 0.53* |
| Vegetated islands sheltered | 7 | 0.98*** | 0.93** | 0.85* | 0.76* |
| exposed | 7 | 0.98*** | 0.95** | 0.86* | 0.79* |
| all | 14 | 0.93*** | 0.93*** | 0.84*** | 0.61* |

Significance of correlation coefficients: ns $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 4

Plant species (S): area (A) relationships for mainland sites and vegetated islands. The correlation coefficients and their significance is shown for the four mathematical models examined

| Places | Sample size | Models | | | |
|--------------------|-------------|---------------|---------------------|------------------|------------------|
| | | <i>S v. A</i> | <i>ln S v. ln A</i> | <i>S v. ln A</i> | <i>ln S v. A</i> |
| Mainland sheltered | 8 | 0.90** | 0.96*** | 0.94*** | 0.73* |
| exposed | 9 | 0.79* | 0.94*** | 0.96*** | 0.71* |
| Islands sheltered | 7 | 0.78* | 0.57 ns | 0.80* | 0.43 ns |
| exposed | 7 | 0.91** | 0.90** | 0.90** | 0.76* |

Conventions as in Table 3

Table 5

Plant species (S): elevation (E) relationships for mainland sites and vegetated islands. The correlation coefficients and their significance are shown for the four mathematical models examined

| Places | Sample size | Models | | | |
|--------------------|-------------|---------------|---------------------|------------------|------------------|
| | | <i>S v. E</i> | <i>ln S v. ln E</i> | <i>S v. ln E</i> | <i>ln S v. E</i> |
| Mainland sheltered | 8 | 0.91** | 0.85** | 0.76* | 0.93*** |
| exposed | 9 | 0.92*** | 0.88** | 0.88** | 0.88** |
| Islands sheltered | 7 | 0.84* | 0.70 ns | 0.85* | 0.51 ns |
| exposed | 7 | 0.96*** | 0.90** | 0.91** | 0.84* |

Conventions as in Table 3

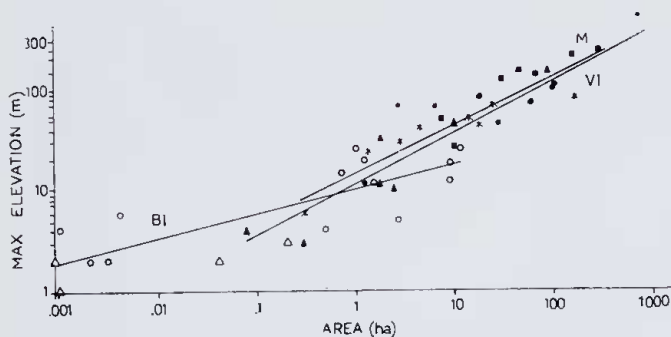


Figure 2.—Double-logarithmic plot of elevation v. area for mainland sites (sheltered *, exposed ■) and islands (sheltered vegetated ▲, sheltered bald △, exposed vegetated ●, exposed bald ○). M, VI and BI represent regression lines for mainland sites, vegetated islands and bald islands respectively.

species. That is, islands of these minimum dimensions are not subject to wave action intense enough to wash away soil forming by subaerial erosion of rock.

Number of plant species v. area (Fig. 3).—The regression line for sheltered mainland sites had a significantly higher slope and intercept than that for the sheltered islands; that for the exposed mainland sites differed significantly in slope only from the regression line for exposed islands. There was no significant difference in slope or intercept for the comparison of regression

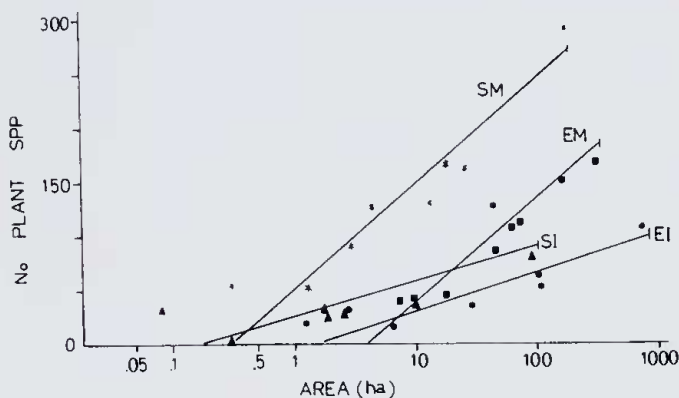


Figure 3.—Relation between number of plant species and \ln area for sheltered mainland sites (SM), exposed mainland sites (EM), sheltered vegetated islands (SI) and exposed vegetated islands (EI). The respective regression equations are $Y = 61.9 + 37.2 \ln X$, $Y = -45.1 + 38.5 \ln X$, $Y = 29.0 + 9.1 \ln X$, and $Y = 3.5 + 12.6 \ln X$.

lines for sheltered islands and exposed islands. However, regression lines for sheltered and exposed mainland sites did differ significantly in intercept but not slope, whereas the lines for exposed mainland sites and sheltered islands differed significantly only in slope.

Number of plant species v. maximum elevation (Fig. 4).—Regression lines for exposed mainland sites and exposed islands differ significantly in slope and in intercept, as do those for sheltered mainland sites v. sheltered islands, and sheltered mainland sites v. exposed mainland sites. There were no significant differences in slope or intercept between sheltered and exposed islands, and between exposed mainland sites and sheltered islands.

The significance of these findings for understanding the transition from mainland site to island is clear from Table 6, for 3 different sized areas. It is necessary to

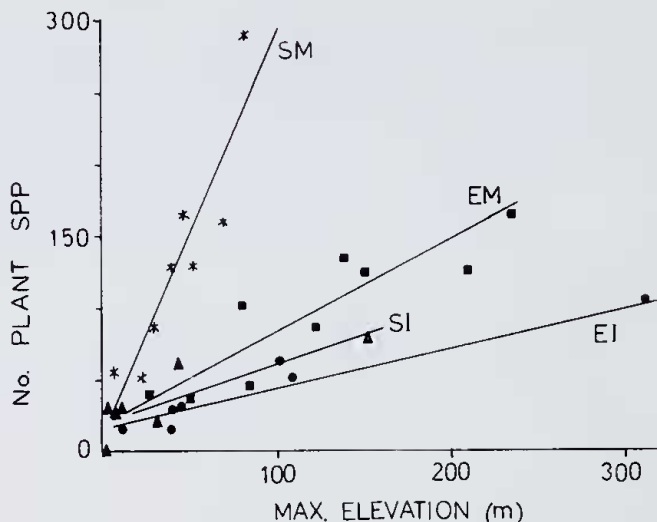


Figure 4.—Relation between number of plant species and elevation for sheltered mainland sites (SM), exposed mainland sites (EM), sheltered vegetated islands (SI) and exposed vegetated islands (EI). The respective regression equations are $Y = 8.6 + 2.9 X$, $Y = 19.6 + 0.6 X$, $Y = 20.7 + 0.4 X$, and $Y = 15.0 + 0.3 X$.

Table 6

Number of species of plants expected to be present on 10, 50, and 100 ha areas on mainland and islands (based on regression equations given in legend to Fig. 3)

| Place | Area (ha) | | |
|--------------------|-----------|-----|-----|
| | 10 | 50 | 100 |
| Mainland sheltered | 148 | 207 | 233 |
| exposed | 44 | 106 | 132 |
| Islands sheltered | 50 | 65 | 71 |
| exposed | 33 | 53 | 62 |

assume that all, or the majority, of the plant species that are at present on the mainland sites occurred there when the islands formed. A sheltered mainland area that through rising sea level becomes a sheltered island should lose about 70% of the plant species present, whereas an exposed island formed from an exposed mainland area should lose 25–50% of its plant species. Because of the nature of the assumption stated above these figures are maxima. Possible reasons for the disappearance of plant species from such islands relative to mainland sites of similar area, elevation and degree of exposure include: freedom from fire; presence of colonially-nesting seabirds; increased exposure to salt spray; and attenuation of re-colonization as species disappear after isolation. These factors will be fully considered later.

Number of species of landbirds

The analysis is similar to that applied above with number of plant species, except that number of plant species itself is an additional variable to area, elevation and degree of exposure. Nevertheless, area gives the highest correlation coefficients (Table 7).

Table 7

Correlation coefficients and their significance for number of landbird species (B) versus area (A), elevation (E), and number of plant species (P). Based on an arithmetic mathematical model

| Place | Sample size | Comparison | | |
|--------------------|-------------|------------|---------|---------|
| | | B v. A | B v. E | B v. P |
| Mainland sheltered | 8 | 0.93*** | 0.82* | 0.96*** |
| Mainland exposed | 9 | 0.97*** | 0.86** | 0.76* |
| Islands sheltered | 7 | 1.00*** | 0.98** | 0.82* |
| Islands exposed | 7 | 0.97*** | 0.97*** | 0.94** |

Conventions as in Table 3.

Because some exposed and sheltered islands and one mainland sheltered site lack landbird species, those mathematical models using log B could not be applied. The semilogarithmic model involving log area, log elevation or log number of plant species gave lower correlation coefficients than the non logarithmic analyses; therefore only the latter are given in Table 7.

Regression lines for number of landbird species v. area are shown in Fig. 5. Those for sheltered and exposed mainland sites differ significantly in slope and intercept, as do those for sheltered islands v. exposed islands, and exposed mainland sites v. exposed islands. The regression line for sheltered islands has a higher slope than that of the line for the exposed mainland sites. The sheltered mainland regression line has a higher intercept than the line for the sheltered islands.

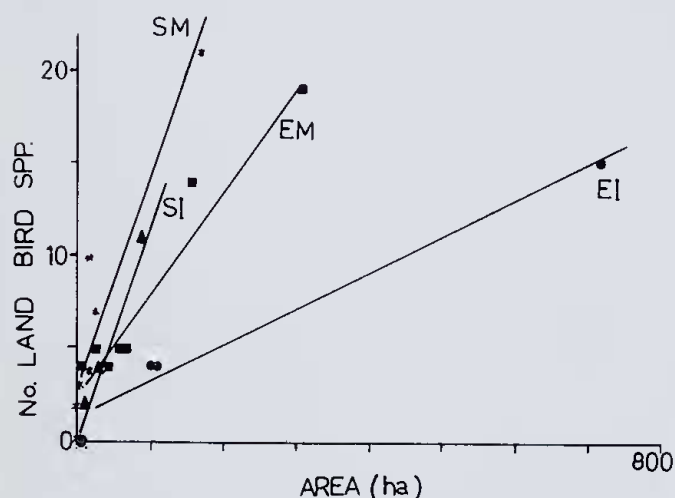


Figure 5.—Relation between number of landbird species and area for sheltered mainland sites (SM), exposed mainland sites (EM), sheltered vegetated islands (SI) and exposed vegetated islands (EI). The respective regression equations are $Y = 2.73 + 0.11 X$, $Y = 2.27 + 0.06 X$, $Y = 0.01 + 0.12 X$, and $Y = 1.15 + 0.02 X$.

The number of species of landbirds that could disappear from mainland sites of 3 different areas as they become islands is given in Table 8. For areas of 100 ha there is a particularly interesting result. The sheltered islands have over 50% more species than the exposed mainland sites. This presumably indicates the greater importance of habitat structure over floristic diversity; the large (100 ha) exposed mainland sites consist mainly of low closed-heath and herbfield whereas the large

Table 8

Number of species of landbirds expected to be present on 10, 50, and 100 ha areas on mainland and islands (based on regression equations given in legend to Fig. 5)

| Place | Area (ha) | | |
|--------------------|-----------|----|-----|
| | 10 | 50 | 100 |
| Mainland sheltered | 4 | 8 | 14 |
| Mainland exposed | 3 | 5 | 8 |
| Islands sheltered | 1 | 6 | 12 |
| Islands exposed | 1 | 2 | 3 |

sheltered islands have forest present on the highest parts and most of the sheltered side. Small (10 ha) exposed mainland sites, however, have more species of landbirds than small sheltered islands. This is both a reflection of inadequate cover on the islands, as well as presumptive high extinction rates and low immigration rates of landbirds (Abbott 1978a).

Percentage frequency of plant species

Quantitative studies of 4 ha plots on the four large islands and one mainland site (a sheltered one on Vancouver Peninsula) reveal that the general impoverishment in plant species already described for total island area exists also at the scale of fifty 1 m² quadrats randomly placed in a 4 ha plot. There are about 2 to 3 times as many species in the 50 mainland quadrats as the island quadrats (Table 10). Even if only those species with frequency of 10% or more are considered, the mainland quadrats still have many more plant species (Table 10).

Distribution patterns

Plant species.—The two most widespread species are *Poa poiformis* (on 17 mainland sites and 11 islands) and *Carpobrotus virescens* (16 mainland sites, 12 islands). These are followed by *Scirpus nodosus* and *Rhagodia radiata* (present on 27 of 31 sites), the introduced *Sonchus oleraceus* (26), *Crassula macrantha*, *Apium prostratum* and *Senecio lautus* (24), *Sporobolus virginicus*, *Lepidosperma gladiatum* and *Samolus repens* (22), *Agonis flexuosa*, *Leucopogon revolutus* and *Olearia axillaris* (21), *Lobelia alata* (20), *Hibbertia cuneiformis* (19), and *Threlkeldia diffusa*, *Anthocercis viscosa* and the introduced *Hypochoeris glabra* (18). These are species able to survive both on islands and mainland. In no case can we say why, because the necessary physiological studies have yet to be made.

Equally interesting are anomalous distribution patterns, in which plant species occur either on many sites, or only on a small subset of sites. The patterns described below could be explained by random immigration or extinction, competitive exclusion, or differences in soil properties between sites. Experimental studies, either in the glasshouse or field, will be necessary before definite conclusions can be drawn.

Banksia praemorsa: Although present on many of the mainland sites, its only insular occurrence is Bald Island. This is also one of the very few island occurrences of the genus in Western Australia.

Callitris preissii: Present only on Bald Island and the adjacent mainland site Q.

Table 9
Summary of analyses of covariance

| Dependent and Independent Variables | Figure | Comparison | Adjusted Independent Variable | Significance of difference between | |
|-------------------------------------|--------|--|-------------------------------|------------------------------------|------------|
| | | | | slopes | intercepts |
| In E, In A | 2 | SM v. EM | 2.9 | ns | ns |
| | | SM v. SI | 1.4 | ns | ns |
| | | SI v. EI | 1.9 | ns | ns |
| | | EM v. EI | 3.5 | ns | ns |
| | | SI v. EM | 2.4 | ns | ns |
| | | EI bare v. EI vegetated all bare islands v. all vegetated islands | 0.25 -0.26 | ns <<0.01 | ns ns |
| P, In A | 3 | SM v. EM | 2.9 | ns | <0.01 |
| | | SM v. SI vegetated | 1.4 | <<0.01 | <<0.01 |
| | | SI veg. v. EI veg. | 1.9 | ns | ns |
| | | EM v. EI vegetated | 3.5 | <<0.01 | <<0.01 |
| | | SI vegetated v. EM | 2.4 | <<0.01 | ns |
| P, E | 4 | SM v. EM | 85 | <<0.01 | <<0.01 |
| | | SM v. SI vegetated | 40 | <<0.01 | <<0.01 |
| | | SI veg. v. EI veg. | 66 | ns | ns |
| | | EM v. EI vegetated | 110 | <0.01 | <<0.01 |
| | | SI vegetated v. EM | 85 | ns | ns |
| B, A | 5 | SM v. EM | 55 | <0.01 | <0.05 |
| | | SM v. SI vegetated | 23 | ns | <0.05 |
| | | SI veg. v. EI veg. | 76 | <<0.01 | <<0.01 |
| | | EM v. EI vegetated | 104 | <<0.01 | <<0.01 |
| | | SI vegetated v. EM | 51 | <0.01 | ns |

A—area, E—elevation, P—number of plant species, B—number of landbird species, SM—sheltered mainland sites, EM—exposed mainland sites, SI—sheltered islands, EI—exposed islands, ns— $P > 0.05$.

Disphyma clavellatum: Occurs only on the most exposed mainland sites and islands, whereas *Carpobrotus virescens* has a much wider distribution. An experimental study of competition in mixtures of the two species under several regimes of salinity would be useful.

Cheilanthes tenuifolia: Present on the 4 largest islands and Mistaken Island, but only occurs on two mainland sites (G, H).

Rhagodia radiata: Present on all mainland sites and on all islands as large as or larger than Mistaken Island, as well as the islet very close to this island. It is, however, absent from Seal Island and Gull Rock.

Agonis flexuosa: Occurs on all mainland sites except L and N and on all medium to large-sized islands except, strangely, Coffin Island.

Chamaelaucium ciliatum and *C. sp. nov.*: Present on the 3 adjacent prominent headlands B, C and O.

Darwinia vestita: Occurs on 3 sheltered mainland sites, one exposed mainland site, and on Bald Island.

Melaleuca lanceolata: Found only on 2 islands (Eclipse, Bald) and on the two adjacent mainland sites (B, Q).

M. microphylla: Similar distribution to *M. lanceolata*, but this species also occurs on a third mainland site, P.

Thryptomene saxicola: Although present on all 4 large islands and found on mainland sites D, H and I, it is unaccountably missing from O and Q.

Logania fasciculata: Found only on 5 exposed mainland sites.

Anthocercis viscosa: Although present on most mainland sites, and on the smaller islands (Mistaken, Coffin, Inner, Gull Rock, Rock Dunder), it is missing from the 4 large islands. In the Archipelago of the Recherche this species does occur on large islands.

Landbirds.—The landbird species with the widest distribution on islands and mainland sites are the Welcome Swallow (present on 20 islands and mainland sites), Silveryeye (20), New Holland Honeyeater (18), White-

browed Scrub-wren (13) and Kestrel (11). However, as indicated in Appendix 2, some of these occurrences are only of presumed vagrants. Considering resident or breeding species of passerine landbirds, 18 of the 31 species were not recorded as breeding or resident on any island. Interestingly, only one of these species (*Sericornis fuliginosus*) is known to occur on islands elsewhere in Western Australia.

Biogeographical considerations proposed for southern Australia by Abbott (1974b) suggest that many of these species were likely to have been present on the islands when they became isolated, but have since become extinct. How could these species have become extinct on the 4 largest islands considered in this paper? Eclipse Island is the oldest and most distant from the mainland and therefore has had more time for extinctions to occur and has given less opportunity for species on the island to immigrate to the island. Michaelmas Island is the youngest, so there has not been so long a time for extinctions to accumulate. Differences in the plant communities between islands are also probably relevant. Why the islands of south-western Australia should have fewer species of landbirds than coastal mainland sites has already been reported on (Abbott 1978a), but why certain species are well represented on islands whereas others are not has not been addressed before for these islands.

The 8 honeyeater species present in the areas studied have broadly similar food preferences (nectar, insects) but only 3 species occur on islands. The New Holland Honeyeater is widely distributed on mainland sites and less so on the islands. I have used my records of feeding sites of this species on the mainland sites near Albany (and elsewhere) to establish which species of flowers it will feed at; I then list which of these plant species occur on the large islands, examine their flowering periods (based on Beard 1970) and attempt to account for the presence/absence of New Holland Honeyeaters on/from the larger islands.

Table 10

Percentage frequency of plant species in six island plots and one mainland plot (based on fifty 1 m² quadrats).
Species with frequency < 10% are omitted.

| Species | Island | | | | | | Mainland Quaranup |
|--|---------|--------|----------|-----------------|--------|--------|----------------------|
| | Eclipse | | Breaksea | Michael- mas | Bald | | |
| | Plot 1 | Plot 2 | | | Plot 1 | Plot 2 | |
| * <i>Ehrlarta longiflora</i> | | | 12 | | | | |
| <i>Danthonia caespitosa</i> | | | | | | 24 | |
| <i>Poa poiformis</i> | | 10 | | | 60 | 48 | |
| * <i>Zantedeschia aethiopica</i> | 74 | | | | | | |
| <i>Carex preissii</i> | | | 22 | | | | |
| <i>Lepidosperma angustatum</i> | | | | | | 14 | |
| <i>L. gladiatum</i> | | | | | 10 | | |
| <i>Scirpus cernuus</i> | | | 16 | | | | |
| <i>S. nodosus</i> | | 16 | | | | 16 | |
| <i>Anarthria gracilis</i> | | | | | | | 10 |
| <i>A. scabra</i> | | | | | | | 66 |
| <i>Hypolaena exsulca</i> | | | | | | | 22 |
| <i>Loxocarya flexuosa</i> | | | | | | | 20 |
| <i>Lyginia barbata</i> | | | | | | | 16 |
| <i>Stypandra grandiflora</i> | | | | | | | 14 |
| <i>Xanthorrhoea preissii</i> | | | | | | | 10 |
| <i>Parietaria debilis</i> | | | 22 | 28 | | | |
| <i>Nuytsia floribunda</i> | | | | | | | 20 |
| <i>Rhagodia radiata</i> | | | 38 | 22 | 24 | | |
| <i>Threlkeldia diffusa</i> | | | | | 18 | | |
| <i>Carpobrotus vivescens</i> | 12 | 82 | 10 | | | | |
| <i>Calandrinia calyptrata</i> | | | | 12 | | | |
| * <i>Stellaria media</i> | | 10 | | | | | |
| <i>Clematis pubescens</i> | | | | 58 | | 14 | |
| <i>Drosera erythrorrhiza</i> | | | | | | | 16 |
| <i>D. pallida</i> | | | | | | | 46 |
| <i>Crassula macrantha</i> | | | 20 | | | | |
| <i>Acacia pulchella</i> | | | | | | | 22 |
| <i>Templetonia retusa</i> | | | | | 24 | | |
| * <i>Geranium molle</i> | | | | 12 | | | |
| <i>Oxalis coriiculata</i> | | | 10 | | 14 | | |
| <i>Chorilaena quercifolia</i> | | | | 12 | | | |
| <i>Amperea ericoides</i> | | | | | | | 28 |
| <i>Phyllanthus calycinus</i> | | | | | 20 | 18 | |
| <i>Spyridium globulosum</i> | | | | | 12 | | |
| <i>Thomasia solanacea</i> | | | | | 24 | | |
| <i>Hibbertia cuneiformis</i> | | | 22 | 20 | | 18 | |
| <i>H. cunninghamii</i> | | | | | | | 12 |
| <i>H. pulchra</i> | | | | | | | 18 |
| <i>Pimelea clavata</i> | | | | | 12 | | |
| <i>Agonis flexuosa</i> | | | | | | | 44 |
| <i>Eucalyptus angulosa</i> | | | | 84 | | | |
| <i>E. calophylla</i> | | | | | | | 48 |
| <i>E. marginata</i> | | | | | | | 22 |
| <i>Melaleuca lanceolata</i> | 38 | | | | 38 | | |
| <i>M. microphylla</i> | 36 | | | | | | |
| <i>M. thymoides</i> | | | | | | | 36 |
| <i>Thryptomene saxicola</i> | | | 54 | | | 38 | |
| <i>Verticordia plumosa</i> | | 14 | | | | | |
| <i>Trachymene pilosa</i> | | | | | | | 24 |
| <i>Andersonia sprengeloides</i> | | 12 | | | | | 16 |
| <i>Astroloua drummondii</i> | | | | | | | 10 |
| <i>Leucopogon oxycedrus</i> | | | | | | | 20 |
| <i>L. revolutus</i> | | | 16 | | | | 18 |
| <i>Lysinema ciliatum</i> | | | | | | | 46 |
| * <i>Anagallis arvensis</i> | | | 24 | | | | |
| <i>Opercularia hispidula</i> | | | | | | | 14 |
| <i>Stylidium adnatum</i> | | 12 | | 22 | | | |
| * <i>Hypochoeris glabra</i> | | | | | | | 26 |
| <i>Millotia tenuifolia</i> | | | | | | | 10 |
| <i>Senecio lantus</i> | | 14 | 50 | 26 | 24 | | |
| No. species with frequency > 10% recorded in fifty 1 m ² quadrats | 4 | 7 | 14 | 10 | 12 | 8 | 27 |
| Total No. species recorded in fifty 1 m ² quadrats | 12 | 13 | 30 | 25 | 21 | 30 | 97 |

* Indicates naturalized alien species.

Eclipse Island has a large area (25 ha) of *Melaleuca lanceolata* and *M. microphylla* with respective flowering periods from August to January and September to October. The absence of New Holland Honeyeaters from Eclipse Island could therefore be explained by a lack of nectar between February and July. Breaksea Island has only a small clump of one plant species that produces suitable food, namely *Agonis flexuosa*. This

flowers between August and December, so the lack of nectar from January to July could account for the absence of New Holland Honeyeaters from Breaksea Island. The remaining 2 large islands have large populations of this species of honeyeater. Food species and their flowering times are as follows—Michaelmas Island: large areas of *Eucalyptus angulosa* (March-August), *Agonis flexuosa* (August-December) and

smaller areas of *Eucalyptus coriuta* (November) and *Agonis marginata* (February-June); Bald Island; large areas of *Melaleuca lanceolata* (August-January), *M. microphylla* (September-October) and *Agonis flexuosa* (August-December) with smaller areas of *Eucalyptus lehmannii* (July-September), *Agonis marginata* (February-June), *Banksia praemorsa* (July-December) and *Calothamnus quadrifidus* (December-July). These last 3 species occur in the open-heath unit (Abbott in prep.). For both Michaelmas and Bald Islands there is virtually all-year round availability of nectar.

Presumably, similar reasoning applies to the other honeyeater species, but their absence from Michaelmas and Bald Islands may result from competitive interactions with the New Holland Honeyeater.

The probable reason that the Silvereye is widely distributed on the islands is that it is ecologically versatile, eating insects, nectar, and small fruits of *Rhagodia*, *Threlkeldia*, *Euchylaena* and *Tetragonia amplexicoma*, all species of plants common in places on the islands.

Why the fourth most widely distributed species, the White-browed Scrub-wren, should be absent from 3 large islands with apparently suitable habitats (Eclipse, Breaksea, Michaelmas) may be explained by reference to mainland site M and Mistaken and Bald Islands. I think that scrub-wrens did once occur on all large islands but became extinct on some of them for reasons unknown. The occurrence of this species on Bald Island suggests that an island of 700 ha area can retain a viable population of scrub-wrens, whereas 100 ha (the approximate area of the other 3 large islands) is too small. The presence of this species on site M, almost detached from the mainland, and on Mistaken Island, only 10 m from the mainland, shows that the species can live on small, close islands or quasi-islands.

Its immigration rate to these islands or quasi-islands must be high, but not high enough to Michaelmas, Breaksea or Eclipse Islands which are over 2 km from the mainland. Diamond (1975) and Abbott (1978a) have provided other evidence emphasizing the real importance of narrow straits as barriers to the movement over water of many passerine species.

The most abundant species on the islands sampled quantitatively (Table 11) were the Silvereye on 3 islands, the New Holland Honeyeater on 2 islands, and the Brown Thornbill and Red-eared Firetail on Bald Island. On the one mainland site sampled the New Holland Honeyeater and Silvereye were most abundant.

Bald and Michaelmas Islands show several marked avifaunal similarities. The Grey Fantail, Golden Whistler, White-breasted Robin, Brown Thornbill and White-naped Honeyeater (possibly only vagrant on Bald Island) occur only on these 2 islands, probably because both islands have extensive areas of forest on them. Michaelmas and Bald Islands are the only islands on which the White-breasted Robin (endemic to Western Australia) occurs.

The spread of weeds

Weeds, i.e. naturalized alien plant species, have only been present in the Albany district since 1826, and hence have had less time to colonize islands than native plant species. On this basis they should be more prominent in coastal mainland areas than on nearby islands. However, coastal mainland soils have low concentrations of phosphorus and nitrogen (Burvill 1965, Donald 1964, Wild 1958), but carry heath communities very rich in plant species (Table 1; Marchant 1973). As many weed species require fertile soils, they may be unable to persist in coastal soils. On islands, in contrast, colonially-

Table 11

Relative abundance of bird species mist-netted on four large islands and on one mainland location

| Species | Island | | | | | | | | Mainland | |
|--------------------------------------|---------------|-------|------------------------|------|---------------|------|--------------|------|----------------|------|
| | Eclipse | | Breaksea | | Michaelmas | | Bald | | Quaranup | |
| | N | RA | N | RA | N | RA | N | RA | N | RA |
| Brown Quail | — | — | 1 | 1.2 | — | — | + | + | — | — |
| Shining Bronze-Cuckoo | — | — | — | — | 4 | 4.3 | — | — | — | — |
| Laughing Kookaburra | + | + | + | + | 2 | 2.2 | + | + | + | + |
| Welcome Swallow | + | + | 1 | 1.2 | 2 | 2.2 | + | + | + | + |
| White-breasted Robin | — | — | — | — | 2 | 2.2 | 1 | 2.5 | 3 | 3.6 |
| Golden Whistler | — | — | + | + | + | + | + | + | 1 | 1.2 |
| Grey Fantail | — | — | — | — | + | + | + | + | 1 | 1.2 |
| White-browed Scrub-wren | — | — | — | — | — | — | 5 | 12.5 | 4 | 4.8 |
| Western Gerygone | — | — | — | — | + | + | — | — | 3 | 3.6 |
| Brown Thornbill | — | — | — | — | 5 | 5.4 | 8 | 20.0 | 2 | 2.4 |
| White-naped Honeyeater | — | — | — | — | 9 | 9.8 | + | + | — | — |
| New Holland Honeyeater | — | — | — | — | 12 | 13.0 | 8 | 20.0 | 33 | 39.8 |
| Brown Honeyeater | — | — | — | — | 2 | 2.2 | — | — | 3 | 3.6 |
| Western Spinebill | — | — | — | — | — | — | — | — | 7 | 8.4 |
| Silvereye | 110 | 100.0 | 84 | 97.7 | 54 | 58.7 | 8 | 20.0 | 26 | 31.3 |
| Red-eared Firetail | — | — | — | — | — | — | 10 | 25.0 | + | + |
| Total No. birds netted | 110 | | 86 | | 92 | | 40 | | 83 | |
| Total No. net-hours | 534 | | 334 | | 381 | | 400 | | 468 | |
| Total No. birds netted/100 net-hours | 21 | | 26 | | 24 | | 10 | | 18 | |
| Total No. species netted | 1 | | 3 | | 9 | | 6 | | 10 | |
| Netting dates | 3-17 April 75 | | 22 Aug.- 2 Sept. 75 | | 3-15 Sept. 75 | | 13-26 May 76 | | 15-25 Sept. 76 | |

- N Number trapped of each species.
- RA Relative abundance (%) of each species trapped.
- + Present but not netted.
- Absent.

nesting seabirds fertilize soils with phosphates and nitrogenous compounds (Gillham 1956). As most weeds and few sclerophyllous species are tolerant of fertile soils (Gillham 1961), weeds should flourish on islands.

Because coastal sites and islands are of unequal area and elevation and consequently have different sized floras (Table 1), it is inappropriate to compare numbers of weed species directly because large areas are more likely to have more weed species. A more valid approach is to list all of the native plant species found on the smallest islands or parts of islands, 49 species in all. These species must be tolerant to exposure to seaspray, a condition characteristic of small islands. It is necessary to assume all species of weeds are capable of establishing on islands. The proportion of weed species present at each site was calculated on the basis of how many of these 49 species and of the 66 weed species were present at each site (Table 12). In the following analyses, statistical significance was determined using the Mann-Whitney test (Siegel 1956).

Table 12

The number of alien plant species on mainland sites and vegetated islands visited

| Code in Fig. 1 | No. of the 49 native plant species suited to survive on small islands occurring on site/island | No. alien plant species | % aliens |
|--------------------------|--|-------------------------|----------|
| Mainland sites | | | |
| A | 23 | 6 | 20.7 |
| B | 25 | 3 | 10.7 |
| C | 22 | 3 | 12.0 |
| D | 22 | 6 | 21.4 |
| E | 19 | 15 | 44.1 |
| F | 18 | 18 | 50.0 |
| G | 24 | 11 | 31.4 |
| H | 31 | 39 | 55.7 |
| I | 18 | 8 | 30.8 |
| J | 23 | 7 | 23.3 |
| K | 19 | 10 | 34.5 |
| L | 18 | 4 | 18.2 |
| M | 17 | 2 | 10.5 |
| N | 19 | 1 | 5.0 |
| O | 21 | 1 | 4.5 |
| P | 16 | 3 | 15.8 |
| Q | 23 | 8 | 25.8 |
| Vegetated islands | | | |
| 8 | 15 | 1 | 6.3 |
| 9 | 23 | 11 | 32.4 |
| 14* | 14 | 9 | 39.1 |
| 15 | 1 | 0 | 0 |
| 16 | 19 | 10 | 34.5 |
| 17 | 24 | 18 | 42.9 |
| 22* | 11 | 19 | 63.3 |
| 23* | 10 | 15 | 60.0 |
| 24 | 30 | 10 | 25.0 |
| 25 | 31 | 17 | 35.4 |
| 26 | 25 | 2 | 7.4 |
| 32 | 17 | 6 | 26.1 |
| 35 | 31 | 8 | 20.5 |
| 36 | 11 | 0 | 0 |

* Indicates islands with colonies of Silver Gulls.
% aliens = $100 \times \text{col. 3} / (\text{col. 2} + \text{col. 3})$.

Coastal sites and islands have similar proportions of weed species ($n_1 = 14$, $n_2 = 17$, $P > 0.05$, 2-tailed test; see Fig. 6 (I)). Even if those sites disturbed by European man (i.e. those with buildings, vehicle tracks, grazing by animals introduced by man) are removed from analysis, no significant difference results ($n_1 = 8$, $n_2 = 10$, 2-tailed $P > 0.05$). Comparison of disturbed coastal sites with undisturbed ones shows that, as expected, disturbed sites have a greater proportion of

weed species ($n_1 = 7$, $n_2 = 10$, 1-tailed $P < 0.01$). However, there is no significant difference in proportion of weed species on disturbed islands as compared with undisturbed ones.

These results can best be explained (Fig. 6 (I)) in the framework of the equilibrium theory (MacArthur and Wilson 1967). Weed species have only been in the Albany district for the last 150 years; some were deliberately introduced for agriculture but most were inadvertent introductions. The source area for colonization of the coastal sites and islands is Albany and the farming areas inland from the coast (Fig. 1). Immigration rates of weed species onto the coastal sites are probably high, because of the closeness of these sites to the source area, and because tracks to fishing places pass through some of the coastal sites so that European man must have introduced some. However, extinction rates of weed species in coastal sites should be high because of low fertility levels in the soil (Specht 1963, Grundon 1972) and possibly through competition for space from the native flora. Immigration rates to the islands are probably low (because of distance from source areas) but extinction rates should be lower than on the mainland as a result of the higher fertility levels of island soils. More knowledge about the phosphorus and nitrogen requirements of the 66 weed species and differences in performance when grown on island and coastal mainland soils would enable precise statements to be made about extinction rates (cf. Rorison 1971). Also, 21 weed species are found only on coastal sites, and 18 only on islands (Appendix I). This probably reflects differences in dispersal abilities and fertility requirements between species.

Up to 8 species of seabirds (Pacific Gull, Silver Gull, Little Penguin, White-faced Storm-Petrel, Crested Tern, Great-winged Petrel, Flesh-footed Shearwater and Little Shearwater) breed on the islands shown in Figure 1 (Abbott 1978b, in press, Kolichis and Abbott 1978, Fullagar and van Tets 1976). Five of these species feed exclusively at sea. A further 2, Crested Tern and Pacific Gull, visit rivers and beaches but rarely venture farther inland. The Silver Gull alone crosses to and from the mainland in large numbers, apparently on a daily basis during the breeding season, and scavenges food from rubbish tips and parks. The 3 islands near Albany with colonies of Silver Gulls (Seal and Green Islands, Gull Rock) have a significantly greater proportion of weed species than the undisturbed islands without gull colonies ($n_1 = 3$, $n_2 = 5$, 1-tailed $P = 0.018$). How Silver Gulls transport weeds is unknown, though Gillham (1956) records that the faeces of 3 gull species present on Skokholm Island (Wales) frequently contained seeds of weeds. On islands with gull rookeries near Perth, the immigration rate of weed species is higher than to islands of comparable size without gull rookeries (Abbott 1977).

In summary, my interpretation is that weed species have higher immigration rates onto coastal mainland sites than onto islands as a result of direct spreading by European man and of proximity to settled areas which are the source areas of weeds. The extinction rate of weed species on coastal mainland sites should be higher than on islands because soil fertility on the former is too low for persistence. The Silver Gull is probably the main vector of weeds to islands because it is the only seabird species near Albany that regularly crosses in large numbers to and from the mainland where they gather at rubbish tips and on lawns in parks, places where weeds are common. These relations are set out in Fig. 6 (II).

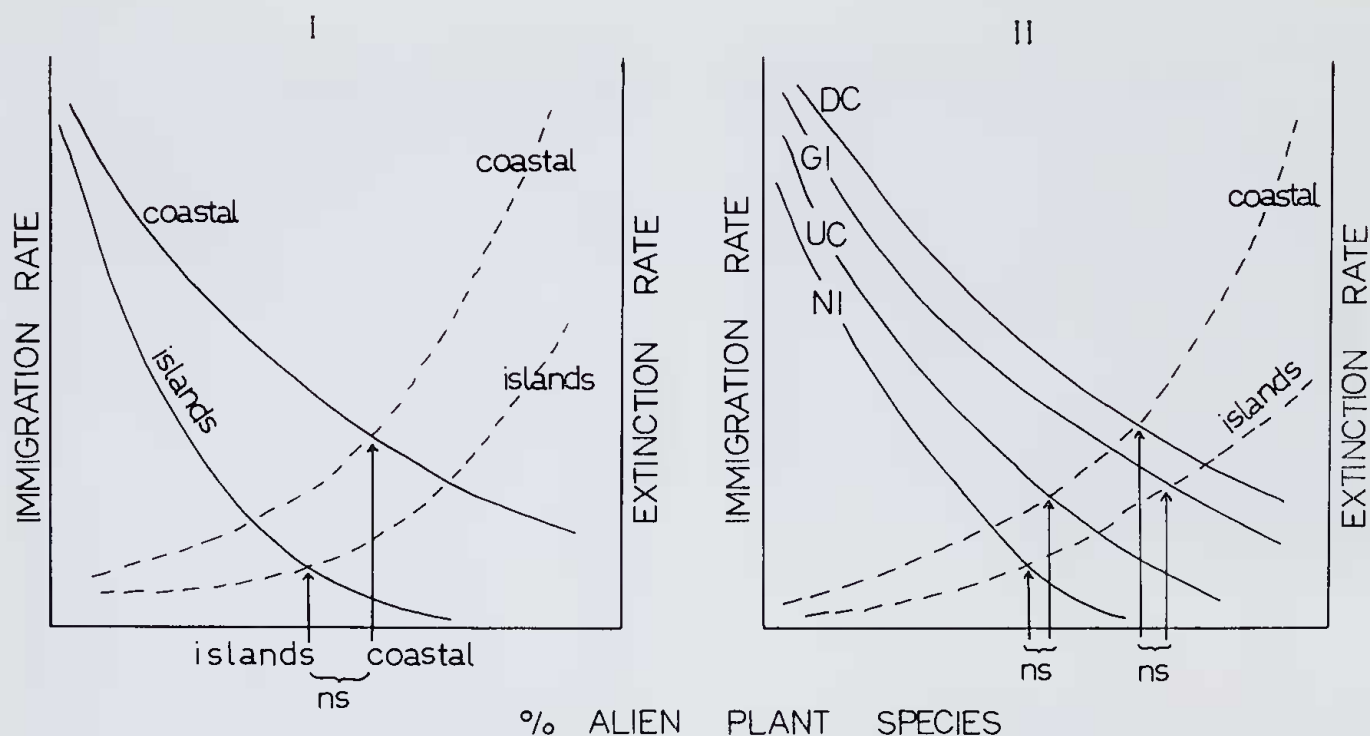


Figure 6.—Proposed model of the proportion of weed (alien plant) species on islands and coastal mainland sites in terms of I. A balance of immigration and extinction rates, II. A balance of both rates taking into account the influence of European man and the Silver Gull. Abbreviations under II: DC, disturbed coastal sites; GI, islands with gull rookeries; UC, undisturbed coastal sites; NI, islands lacking gull rookeries. ns, not significant ($P > 0.05$).

Discussion

Possible causes of differences between plant communities

Three factors, degree of exposure, presence of nesting seabirds, and relative freedom from fire, at face value are important in explaining floristic and vegetation differences between islands and coastal mainland sites (Abbott and Black 1978). The area of an island and its maximum elevation jointly determine how severe wave action will be to the island environment. If the island is too small or too low, storm waves will wash over the island removing soil and vegetation. This will not happen to islands of sufficiently large area and of high elevation, but the weather side will have more bare rock and prostrate halophyte-dominated vegetation than the lee side. The sheltered side will probably have large areas of taller vegetation. In contrast, exposed mainland sites will generally lack tall vegetation unless valleys or large hills are present in which case small areas of taller vegetation can develop.

Many plant species are unable to survive high levels of salt on their leaves (Parsons and Gill 1968). This leads to zonation both on islands and mainland. Exposed mainland sites have a wide zone of salt-tolerant species near the coastline whereas on sheltered mainland sites this zone is a narrow one, occurring just above high water mark. Small, low, exposed islands generally show no zonation because most of their plant species are halophytic.

Because seabirds almost exclusively nest on islands, the manurial effect of their guano on island soils leads to differences in species composition between islands and mainland. Many sclerophyllous species are unable to survive and weeds establish and flourish (Gillham 1960). The influence of degree of exposure to saltspray and density of seabirds outlined in a scheme for several islands in the Archipelago of the Recherche (Abbott

and Black 1978, p. 121) appears to apply validly to the Albany islands considered in this paper. There are of course differences in representation by various species, as some in the Albany district do not extend as far east as the Esperance district and vice-versa; also the halophytic genus *Atriplex* is poorly represented in the Albany area.

Rarity of fires on islands has probably had more effect on floristic composition than vegetation structure. It probably has allowed the development and survival of certain monospecific plant communities, for example *Melaleuca* forests on Eclipse and Bald Islands and on other islands round the south-western Australian coast (e.g. Rottnest, Garden). Low frequency of fires on islands may account largely for species impoverishment. Russell and Parsons (1978) have shown that in coastal heaths in Victoria species richness declines with time since the last fire by about 15% in 20 years. Lack of fire probably alters the competitive advantage amongst plant species in a community, particularly as it pertains to the recruitment of seedlings into the community. On islands, the recolonization of species lost by lack of fire is probably mainly determined by the distance of the island from the mainland.

It is, however, difficult to stress any one of these 3 factors just considered. The first 2, degree of exposure to seaspray and presence of nesting seabirds, are probably more important in explaining floristic and vegetation differences between islands, whereas the presence of nesting seabirds and the infrequency of fire on islands seem more important in accounting for differences between islands and mainland, as the following example shows. Mistaken Island is burrowed, where soils are deep enough, by Little Penguins. The island is sheltered from prevailing winds and sea and supports vegetation up to 6 m tall. Nearby mainland area G (Fig. 1) is

at the end of a peninsula, is of similar rock type, soil type, exposure and elevation but of course lacks nesting seabirds and was no doubt frequently burnt by aborigines. This mainland site has many of the elements of species-rich coastal heath near Albany including *Darwinia diosmoides*, *Lhotskya erieoides*, *Melaleuca thymoides*, *Agonis flexuosa*, *Eucalyptus* spp. whereas Mistaken Island is dominated by *Agonis flexuosa* and to a lesser extent by *Pimelea elavata*, *Acacia eyelops*, *Anthocercis viscosa* and the alien grass *Ehrharta longiflora* (Appendix 1). These two places afford one of the two most striking comparisons known to me. The other is between Breaksea Island (*Rhagodia*-dominated vegetation) and nearby Flinders Peninsula (species-rich open-heath).

An experimental approach, simulating the effect of seabirds on a coastal mainland plot, and of repeated fires on an island plot, seems necessary to distinguish the relative contribution of the fire and seabird factors.

Large-footed surface-nesting species of seabirds, particularly the Pied Cormorant which is so abundant on some of the islets near Fremantle (Abbott 1977), are absent from the islands of the Albany region. Sea lions are now very scarce on the islands covered in this paper although before the 1820s they may have had some effect on the vegetation of Seal Island (Abbott 1979). Hence for the islands near Albany it is unlikely that plant communities were subject to the destructive effects of seabirds and seals.

Possible causes of differences between landbird faunas

I have shown in a general study of islands round south-western Australia that not only do large islands have more species of landbirds than small ones but island habitats also have fewer species of landbirds than coastal mainland habitats of similar structure (Abbott 1978a). I interpreted these facts to mean that once species of landbirds became extinct on islands, they are unlikely to succeed in re-establishing because of their low vagility. In this paper I have suggested that this same argument applies to the White-browed Scrub-wren, whereas there is reasonable evidence to indicate that the New Holland Honeyeater may be absent from certain large islands because a year-round supply of nectar (as suggested by the flowering phenology of species) is unavailable. This argument may also apply to several other species of honeyeaters. Probably those species of landbird dependent on plant resources such as nectar, fruit and seeds for food will be absent from islands that do not supply such favoured items in sufficient quantity all year.

It is important when comparing island and mainland landbird faunas that habitats of similar structure are considered. Michaelmas Island has more species of landbirds than several adjacent mainland sites solely because its lee side possesses forest in contrast to the mainland sites which are too exposed to support anything but heath.

Impact of European man

Plants.—Although 2 early botanists (G. Maxwell, L. Preiss) collected plants from Breaksea and Mistaken Islands respectively, neither attempted to list the total flora. Thus, with no baseline, it is not possible to evaluate European man's effect on the abundance of native plant species on the islands. His impact on the mainland coast, through the introduction of exotics, is probably similar to that described for a coastal mainland site near Melbourne (Kirkpatrick 1974). His effect through grazing and firing is better understood, and has

already been outlined (see also Kirkpatrick 1975). Settlement at Albany has probably allowed the Silver Gull population to increase substantially over levels before 1826. As this species is probably the chief vector of weeds to their nesting islands, their increase has probably speeded up the colonization of weeds to islands.

The long-term influence of rabbit populations on vegetation on Breaksea, Michaelmas, Eclipse and Mistaken Islands, placed on these islands well before the species crossed to Western Australia from eastern Australia, is unknown. It is likely to be similar to that described for Carnac Island (Abbott 1980).

Landbirds.—The extinction of several landbirds is due to the activities of European man last century, mainly sealers on the islands and settlers on the mainland. Because full lists were not made on my mainland areas, it is difficult to be certain which species may have then been present. Probably *Dasyornis braehypterus* and *Atrichornis clamosus* occurred on several of the sites. Although for the region depicted in Figure 1 both species are known at present to be most abundant on the Mt Gardner promontory, it is invalid to suppose the habitats they occur in there are necessarily their preferred ones or the only ones they can survive in. Rather, a change in fire regime from Aboriginal man to European man may have been responsible (Smith 1977b). I suspect that the Rock Parrot was more widely distributed on the mainland than now; I found this species in small numbers only on 3 mainland sites.

Known extinctions of landbirds on islands (with earlier references to their occurrence) are as follows:—Breaksea Island: Brush Bronzewing (Lockyer 1827) Little Grass Bird (Campbell 1900); Mistaken Island: Brush Bronzewing (Clark 1841), Red-eared Firetail, Brown Thornbill, White-breasted Robin, Sacred Kingfisher (Carter 1909) (Several of the last 4 species may have been vagrants only); Michaelmas Island: Grey Currawong (Bassett Hull 1922), though possibly only a visitor; Green Island: Rock Parrot (Vancouver 1801, King 1827, p. 130).

Rock Parrots were found by me in large numbers only on Coffin Island. Brown Quail were abundant on Bald and Breaksea Islands, particularly on the latter, whereas they seemed to be absent from my mainland sites. Feral cats and foxes on the mainland sites may be responsible for this difference.

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